

The gametogenic cycle of *Brachidontes exustus* (Linné, 1758) (Bivalvia: Mytilidae) at Wassaw Island, Georgia

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Abstract: The gametogenic cycle of a population of *Brachidontes exustus* (Linné, 1758) was studied from January to December 1993 at the northern beach of Wassaw Island, Georgia. Staging values were assigned for Gonadal Indexing (GI) of histologically prepared gonadal tissue: 1 = spent; 2 = partially spawned; 3 = early active; 4 = late active; 5 = ripe. From January to March and September to December, males had significantly higher (ANOVA, $p = 0.0249$) GI values when compared to females. Because male and female GI showed no significant difference (ANOVA, $p = 0.1244$) over the major reproductive period (April to August), they were averaged per sample period. Rapid gonadal development occurred from March to mid-May and follicles were ripe by mid-July. A minor spawn might have occurred in late July. A major spawn occurred from September to November. Of 261 animals sampled, the sex ratio was significantly different (Chi-square = 7.48; $p < 0.05$) from parity (1.00 female:1.43 male) and 9.6% were sexually undifferentiated. The greatest percentage of sexually undifferentiated individuals occurred in March (66.7%) with fewer from January to April. No hermaphrodites were observed.

Key words: *Brachidontes*, gametogenesis, mussel, reproduction, sex ratio

Brachidontes exustus (Linné, 1758), commonly inhabits rock pilings, sea walls, and wharf pilings in the intertidal zone and is most abundant in lower intertidal regions (Seed, 1980). The mussel ranges in the United States from North Carolina to Texas (Abbott, 1974). Information concerning species of *Brachidontes* is limited. Studies include life habitats (Seed, 1980), surface and shell morphology (Fuller and Lutz, 1988, 1989), and larval development (Campos and Ramorino, 1980; Fields and Moore, 1983). In addition, Morton (1988) studied the reproductive cycle of *B. variabilis* (Krauss, 1848) in a Hong Kong mangrove and showed that juveniles grew rapidly, are sexually mature at one-year of age, and had a short life span (< 3 years). Gametogenesis in *B. variabilis* was initiated in winter with individuals spawning in summer and being spent by October-November (Morton, 1988).

Gametogenic cycles have been studied in other marine mussels including *Geukensia demissa* (Dillwyn, 1817) (Heffernan and Walker, 1989; Borrero, 1987; Brousseau, 1982); *Modiolus capax* (Conrad, 1937) (Aguirre and Ramirez, 1989); *Modiolus metcalfei* (Hanley, 1843) (Lopez and Gomez, 1982); *Modiolus modiolus* (Linné, 1758) (Seed and Brown, 1977; Jasim and Brand, 1989); *Modiolus philippinarum* (Hanley, 1843) (Walter and Cruz, 1980); *Mytilus edulis* (Linné, 1758) (Seed and Brown,

1977; Brousseau, 1983); and *Perna picta* (Born, 1778) (Shafee, 1989). Gametogenic studies of species in the southeastern U. S. include comparisons of *G. demissa* populations in South Carolina (Borrero, 1987), an energy flow study of a *G. demissa* population at Sapelo Island, Georgia (Kuenzler, 1961), and a study of reproduction in *G. demissa* at Wassaw Sound, Georgia (Heffernan and Walker, 1989).

There is little information on the life history of *Brachidontes exustus* and no gametogenic study. The purpose of this study was to determine the gametogenic cycle of a population of *B. exustus* at Wassaw Island, Georgia, through histological examination.

METHODS

Between 15 and 20 individuals of *Brachidontes exustus* (1-2 cm in length) were collected monthly from January to March 1993, biweekly from April to September 1993, and monthly from November to December 1993, from the northern beach of Wassaw Island, Georgia (Fig. 1). Inclement weather prevented an October 1993 sampling. Individuals occurred at the base of dead oak trees on the shoreward side within the intertidal surf zone.

Shell length (distance anterior-to-posterior) was

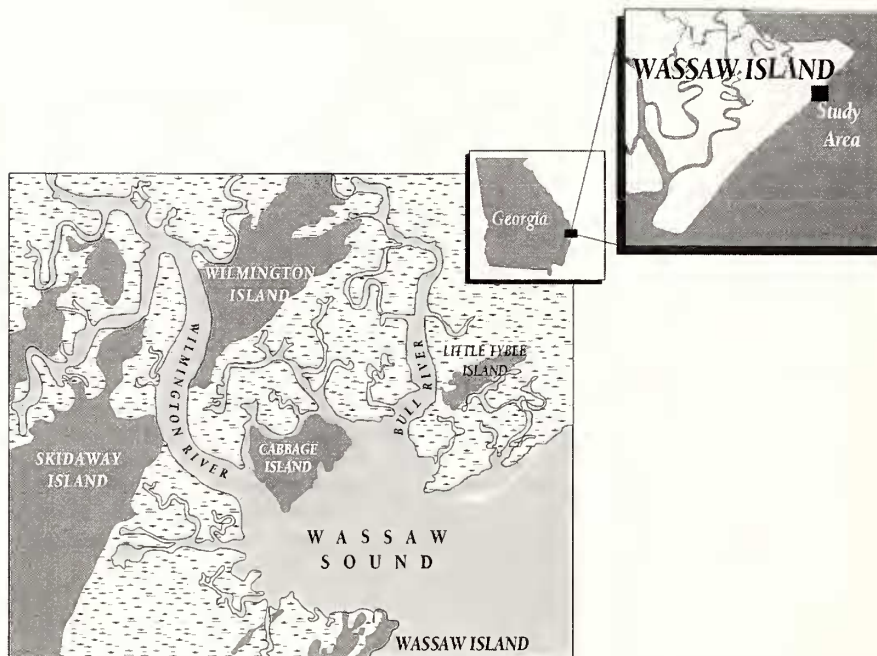


Fig. 1. Location of *Brachidontes exustus* population occurring at the base of dead oak trees in the intertidal surf zone on Wassaw Island, Georgia.

determined using Vernier calipers. The visceral mass was fixed in Davidson's solution (Humason, 1967) for 48 hr, rinsed in 50% alcohol overnight, and stored in 70% alcohol. Tissue samples were dehydrated in a graded alcohol series, cleared in toluene, and embedded in Paraplast®. Paraffin blocks were sectioned (7-8 μm) with a Leica 820 II Microtome. The tissue sections were deparaffinized with toluene, rehydrated to water, and then stained with Harris, Hematoxylin and counterstained with Eosin (Bancroft and Stevens, 1982). Slides were examined and photographed under a light microscope.

Gonadal tissue was rated according to characteristics of gametes and stage of maturity, as described for other species (Brousseau, 1982, 1983; Heffernan and Walker, 1989). Gonadal tissue also occurred in the mantle of all individuals. The gametogenic cycle was divided into the following categories:

Sexually Undeveloped = 0. No male or female gametes detected. Follicles small and shrunken with little or no lumen.

Male Developmental Stages:

Spent = 1. Follicles empty with a large lumen space. A few spermatozoan cells scattered throughout the follicle. Gonads appear much smaller than those in ripe individuals. Blood cells present in the follicles (Fig. 2a).

Partially spawned = 2. Most follicles with the clear lumen surrounded by clusters of spermatozoa (Fig. 2c).

Early active = 3. A narrow-to-wide band of large cells (spermatogonia and/or spermatocytes) located inside

each testis follicle. No smaller spermatids or spermatozoa cells present. Follicle lumen large and devoid of cells (Fig. 2e).

Late active = 4. A wide band of larger cells (spermatogonia and spermatocytes) present along the inside of the testis follicle. Lumen small to nonexistent. Some follicles with small pink streaks. Smaller spermatozoa present toward the center of the follicle (Fig. 2g).

Ripe = 5. Gonads full of spermatocytes, spermatids, and spermatozoa, making it difficult to differentiate cell types. Follicles stained black to dark purple with pink streaks in the center (Fig. 2i).

Female Developmental Stages:

Spent = 1. Follicles mostly empty with only a few scattered oocytes. Blood cells present; follicles smaller than when ripe (Fig. 2b).

Partially spawned = 2. Most of the oocytes mature, each with a large nucleus; many eggs unattached to the follicle wall. Lumen space large. Many follicles with a few or no mature oocytes (Fig. 2d).

Early active = 3. Follicle lumen devoid of cells. Young oocytes with small nuclei attached to the follicle wall (Fig. 2f).

Late active = 4. Oocytes large, elongate, some attached to the follicle wall. Follicles with several mature oocytes present but lumen incompletely filled with eggs (Fig. 2h).

Ripe = 5. Many large mature oocytes present; in most specimens the lumen space is filled. A few oocytes

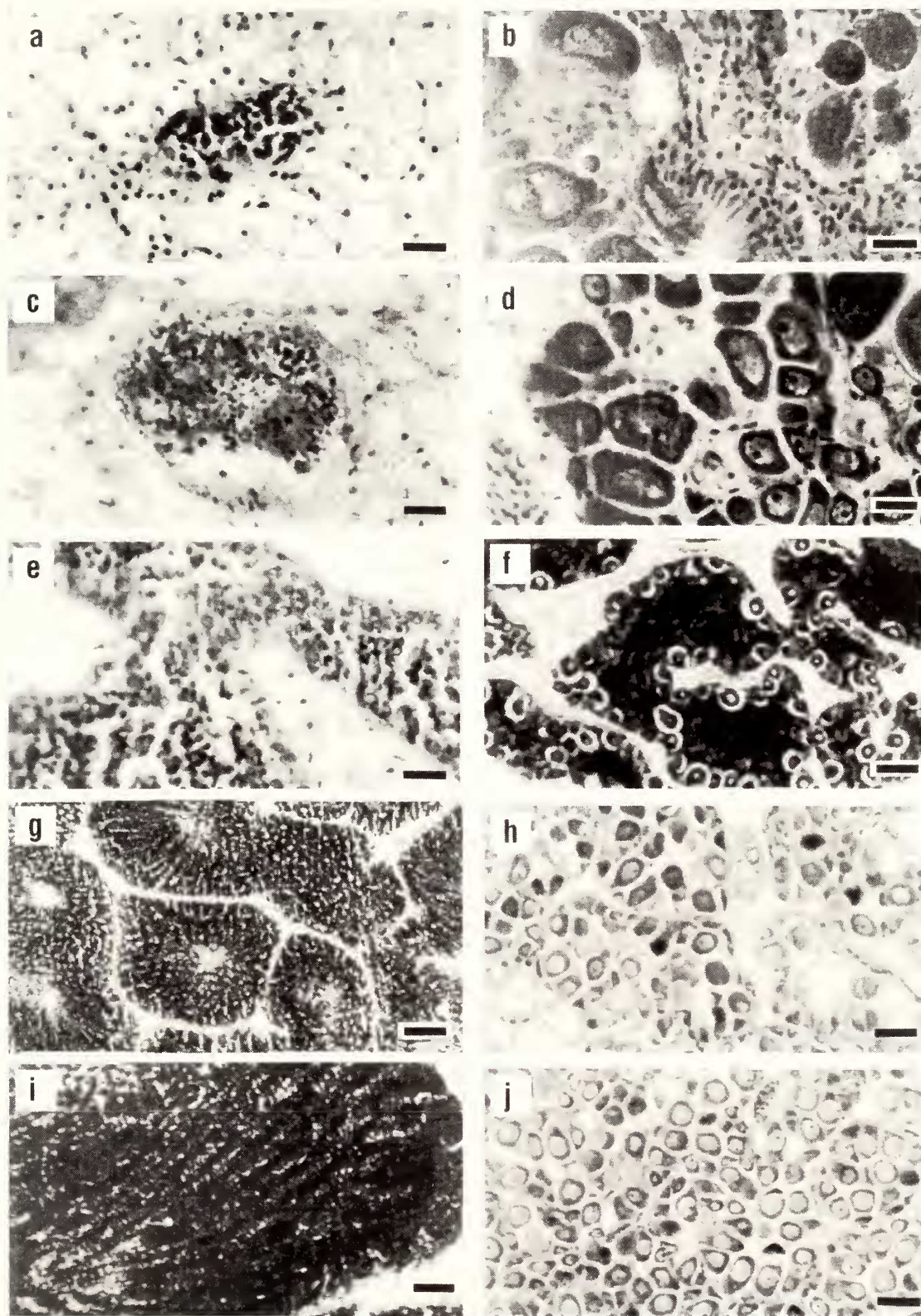


Fig. 2. Reproductive stages in male and female *Brachidontes exustus*: a. Spent male. b. Spent female. c. Partially spawned male. d. Partially spawned female. e. Early active male. f. Early active female. g. Late active male. h. Late active female. i. Ripe male. j. Ripe female. Scale bars = 20 μm (a, b, c, d, e, g, i) or 50 μm (f, h, j).

attached to follicle wall (Fig. 2j).

The sex of each individual was determined and the sex ratio of the population (biweekly sample size, $N = 15$) was tested for non-parity by Chi Square analyses (Elliott, 1977). Statistical analyses of male and female gonadal index values were analyzed by Analysis of Variance (ANOVA) ($\alpha = 0.05$) using SAS for PC computer (SAS Institute, 1989). T-tests ($\alpha = 0.05$) (SAS Institute, 1989) were performed on gonadal index values and shell length data to determine if significant differences occurred at any specific time period.

RESULTS

Individuals varied in shell length from 11.3 to 24.6 mm (mean = 17.3 ± 0.15 mm SE; $N = 261$). A total of 261 mussels were sexed with 9.6% sexually undifferentiated, 37.2% female, and 53.2% male. Sex ratio was significantly different from parity (Chi-square = 7.48; $p < 0.05$) with a ratio of 1.00:1.43 female to male.

Female and male gonadal indices are presented in Fig. 3. ANOVA revealed that males had significantly ($p = 0.0249$) higher GI values over time than females. Males had significantly higher GI values, as determined by T-tests from January to March and from September to December. No significant difference (ANOVA; $p = 0.1244$) in GI value occurred between males and females from April to August. Males had a longer gametogenic cycle than females. Females showed a more rapid drop in GI value ($N = 7$, mean = 4.86 ± 0.14 ; $N = 6$, mean = 1.83 ± 0.65) over males ($N = 8$, mean = 5.00 ± 0.00 ; $N = 9$, mean = 3.67 ± 0.53) during peak spawning (August-September).

Gonadal development was evident throughout

most of the year, except March. The lowest mean GI value for males, females, and sexually undifferentiated individuals combined occurred in March ($N = 15$, mean = 0.58 ± 0.29 ; Fig. 4), during which the highest percentage of undifferentiated animals (66.7%) occurred. The mean GI for males and females combined increased from March ($N = 15$, mean = 0.58 ± 0.29) to April ($N = 15$, mean = 2.27 ± 0.38) and reached a peak in mid-July ($N = 15$, mean = 4.79 ± 0.29). By mid-July, 92.9% of the population was ripe and 7.1% was partially spawned. Low percentages of individuals in the partially spawned stage occurred from May to July (Fig. 4), which could be representative of dribble spawning, *i. e.* when males and females continually produce and release sperm and egg cells, respectively. Indications of spawning were not reflected in mean GI values (Figs. 3-4) during May to July. The combined mean GI value for males and females increased to 4.31 in mid-August, with 76.9% ripe individuals and 23.1% at the partially spawned stage. The highest GI value ($N = 15$, mean = 4.93 ± 0.07) was reached in late August when 93.3% of the sampled population was ripe and 6.7% were spent. A major spawn commenced in early September when there was a decrease in mature gametes ($N = 15$, mean GI = 4.25 ± 0.39). Spawning continued until December ($N = 21$, mean GI = 1.95 ± 0.43) when 40% was spent, 15% was partially spawned, 20% was undifferentiated, and 25% was at the ripe stage (Figs. 4-5).

DISCUSSION

The gametogenic cycle of *Brachidontes exustus* from a population in coastal Georgia showed a unimodal

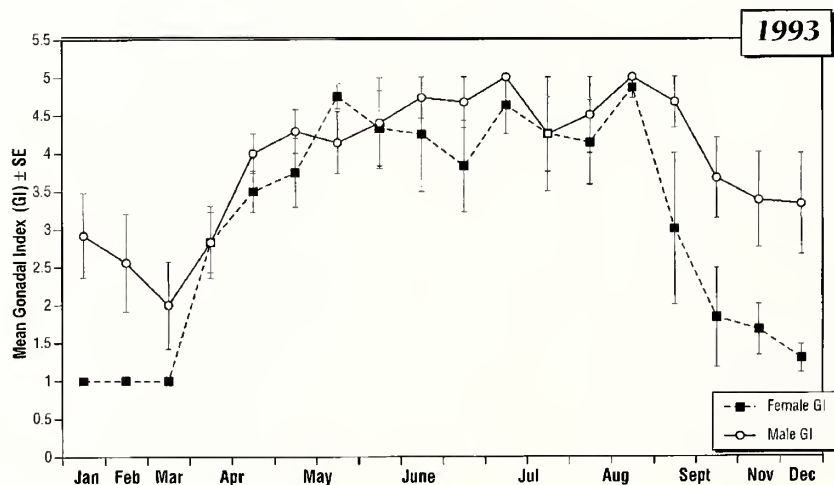


Fig. 3. Mean monthly gonadal index values \pm SE for male and female *Brachidontes exustus* collected at Wassaw Island, Georgia.

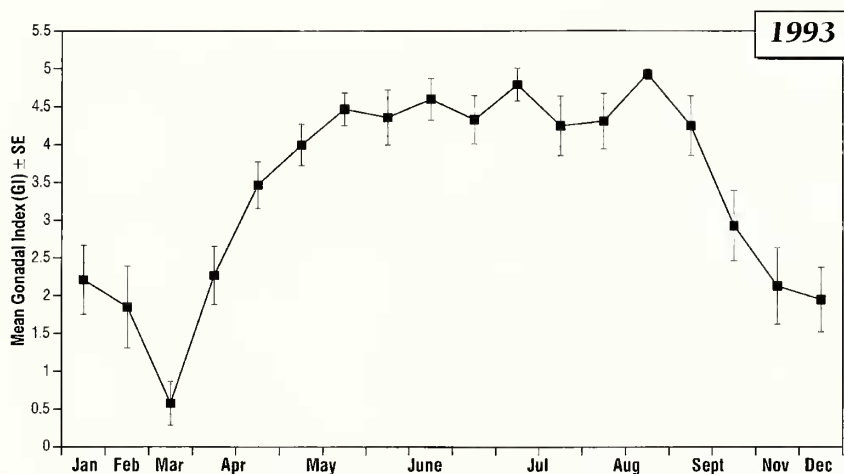


Fig. 4. Mean monthly mean gonadal index values combined for male and female *Brachidontes exustus* collected at Wassaw Island, Georgia.

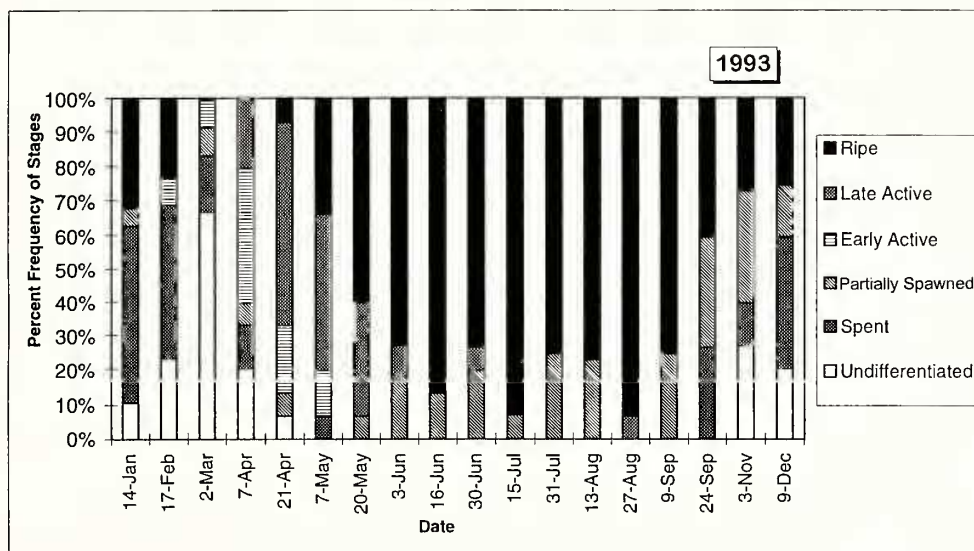


Fig. 5. Relative frequency of gonadal stages over time in *Brachidontes exustus* collected at Wassaw Island, Georgia.

pattern (Figs. 3-4) during 1993, when gamete production increased from March until July, with a major spawn occurring in August and September. Dribble spawning occurred from May to August (Fig. 4) and this phenomenon was similar to the spawning pattern observed in *Mytilus edulis* (see Brousseau, 1983). Brousseau (1983) attributed dribble spawning as a response to variations in environmental conditions over a period of time. The spawning period (August-September 1993) of *B. exustus* at Wassaw Island showed similarities to a *Geukensia demissa* population in Georgia, which spawned from August to October 1984 and July to September 1985 (Heffernan and Walker, 1989). The results of the present study were also similar to Kuenzler's (1961) results (spawning July-September) for a population of *G. demissa* on Sapelo Island, Georgia, and to those of a

study of a population of *G. demissa* at North Inlet Estuary, South Carolina (Borrero, 1987). Borrero (1987) showed that individuals from low intertidal areas increased in gonadal development from May to early August, with a minor spawn occurring in June and a major spawn from August through September. However, a longer spawning period, resembling our results, occurred in a Hong Kong mangrove population of *B. variabilis* (see Morton, 1988). Morton (1988) found that the population of *B. variabilis* ripened in the summer and by November and December 1985, the population was spent.

The lowest mean gonadal index value in March (0.58 ± 0.29) for *Brachidontes exustus* was followed by an increase throughout the spring until peak values were attained in July (mean = 4.79 ± 0.21). The increase in

Table 1. Habitat, sex ratio, and percent hermaphrodites of various mytilid mussels. (E, estuarine; D, deep sea; M, marine; ND, not determined).

Species	Habitat	N	Female/Male	% Herm.	Source
<i>Brachidontes exustus</i>	M	261	1.00:1.43*	0	This Study
<i>B. variabilis</i>	E	247	0.80:1.00	ND	Hulings, 1986
<i>B. variabilis</i>	E	330	1.00:0.69*	0	Morton, 1988
<i>Choromytilus meridionalis</i> (Krauss, 1848)	M	700	0.75:1.00*	0	Griffiths, 1977
<i>Crenomytilus grayanus</i> (Dunker, 1882)	ND	ND	1.00:1.00	ND	Dolgov, 1985
<i>Geukensia demissa</i>	E	354	1.00:1.00	ND	Brousseau, 1982
<i>G. demissa</i>	E	429	1.00:1.00	0	Borrero, 1987
<i>G. demissa</i>	E	498	1.00:1.00	0	Heffernan and Walker, 1989
<i>Idas argenteus</i> (Jeffreys, 1876)	D	101	1.00:0.83	0	Dean, 1993
<i>Lithophaga bisulcata</i> (d'Orbigny, 1842)	M	157	1.00:1.00	ND	Scott, 1988
		96	1.00:1.00	ND	
<i>L. nigra</i> (d'Orbigny, 1842)	ND	231	1.00:0.91	ND	Barkati and Asif, 1984
<i>Modiolus barbatus</i> (Linné, 1758)	ND	975	1.00:1.41	ND	Cahour and Lucas, 1968
		1060	1.00:1.66	ND	
<i>M. metcalfei</i>	E	1280	1.00:1.00	0.16	Lopez and Gomez, 1982
<i>M. modiolus</i>	M	5965	1.00:1.00	**	Jasim and Brand, 1989
<i>M. philippinarum</i>	ND	848	1.00:1.00	ND	Walter and Cruz, 1980
<i>Mytella guyanensis</i> (Lamarck, 1819)	ND	388	3.47:1.00*	ND	Sibaja, 1986
<i>Mytilus edulis</i>	ND	ND	1.00:1.18	ND	Coe, 1943
<i>M. edulis</i>	M	14,661	1.00:1.13*	ND	Seed, 1969
<i>M. edulis</i>	M	534	1.00:1.00	0.02	Brousseau, 1983
<i>M. edulis</i>	ND	3000	1.00:1.00	ND	Dolgov, 1985
<i>M. edulis</i>	ND	450	1.00:0.90	0	Sprung, 1983
<i>M. edulis</i>	M	346	1.00:0.79	0.3	Kautsky, 1982
<i>M. galloprovincialis</i> (Lamarck, 1819)	ND	ND	1.00:1.00	ND	Kudinskii and Shurova, 1990
<i>Perma perna</i> (Linné, 1758)	ND	275	1.00:1.00	0	Lasiak, 1986
<i>P. picta</i>	ND	800	1.00:1.20*	ND	Shafee, 1989
<i>P. viridis</i> (Linné, 1758)	M		1.00:1.00	0	Barkati and Ahmed, 1974
		648	1.00:0.98	0	
			1.00:0.79	0	
<i>P. viridis</i>	ND	1000	1.00:1.00	0	Walter, 1982
<i>P. viridis</i>	ND	1760	1.00:0.78	ND	Vakily <i>et al.</i> , 1988
<i>P. viridis</i>	ND	526	1.00:1.29	<0.1	Lee, 1988
<i>Perumytilus purpuratus</i> (Lamarck, 1819)	ND	797	1.00:1.00	ND	Lozada and Reyes, 1982
<i>Septifer virgatus</i> (Wiesmann, 1837)	ND	382	1.00:0.78	0	Morton, 1995
<i>Xenosirobus securis</i> (Lamarck, 1819)	E	354	1.00:0.91	ND	Wilson, 1969
		316	1.00:0.84	ND	

* Reported to be significantly different from a 1:1 ratio by a Chi-Square test.

** Percent hermaphrodite not determined, but stated in text that some hermaphrodites were observed.

gonadal development during spring reflects the pattern of gametogenesis reported for *Geukensia demissa* populations in Georgia by Heffernan and Walker (1989). The highest percentage of sexually undifferentiated *B. exustus* (66.7%) occurred in March. Sexually undifferentiated mussels occurred in lower percentages during January (10.5%), February (23.1%), April (20.0%), November (26.7%), and December (20.0%) (Fig. 5). Heffernan and Walker (1989) found that during February 1984, 50.1% of the *G. demissa* sampled were sexually undifferentiated. Also, a higher percentage of undifferentiated *G. demissa* occurred in the winter months (November 90% and December 60%), followed by decreasing proportions of undifferentiated animals, and an increase in sexually developing individuals throughout

the spring (Heffernan and Walker, 1989).

Within Mytilidae, sex ratios vary substantially (Table 1). In this study, *Brachidontes exustus* had significantly fewer females than males (1.00:1.43). For *B. variabilis*, Hulings (1986) found that significantly more males occurred in a population in the Gulf of Aqaba (Red Sea), while Morton (1988) found greater number of females than males in a Hong Kong estuarine population.

As with most members of the Mytilidae, *Brachidontes exustus* is dioecious and exhibits stable gonochronism. No hermaphroditic *B. exustus* were found. Hulings (1986) and Morton (1988) observed no hermaphrodites for *B. variabilis*. Within the Mytilidae, hermaphroditism is a rare event (Table 1).

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